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ECOLOGY, LIFE HISTORY AND DISTRIBUTION OF *PALINGENIA LONGICAUDA* (OLIVIER) (EPHEMEROPTERA)

by

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Dedicated to the memory of the Dutch naturalist Jan Swammerdam, who initiated the studies on the life history of Palingenia longicauda *with great love and dedication in 1667*

Abstract

The ecology and life history of *Palingenia longicauda* (Olivier) have been studied in the Bulgarian section of the river Danube, both for the aquatic larval stages and the flying adult stage. The significance of this species for the fisheries is outlined. The distribution in Europe, the retreat from Western Europe and finally the complete disappearance from the Danube river system are described.

Introduction

The first record of mayflies, as well as an explanation of their name was given by Aristoteles (384—322 B.C.) in his Historia Animalium (see Illies, 1968; Francissen & Mol, 1984). Swammerdam (1752: 100) was correct in assuming that Aristoteles, later cited by Plinius and Elianus, had studied the same insect, calling it *Hemerobius*, *Ephemerus* and *Diaria*, respectively.

Clutius (1634) wrote about the abundance of *Hemerobius* in Dutch rivers some 350 years ago. He drew somewhat distorted pictures of the larva (in dorsal and ventral view), of the exuviae and of the adult.

Swammerdam (1675) was the first, who reported on the life history of the larva and of the adult, which he called "Haft" of "Oeveraas", and presented pictures and descriptions of both. They were later included in the Dutch edition of the "Bible of Nature" (Bijbel der Nature) by Swammerdam (1737) — the first book of this kind and of primary importance for that time. In 1752 it was translated into German, and in 1758 into English. Marsili (1726: 25) in his six volumes with geographical, historical, astronomical and hydrographical data on Hungary and the Balkans, reported on the mass flight of this mayfly species over the Tissa river.

At present the nomenclature of this species is as follows:

Ephemera longicauda Olivier, 1791
Ephemera flos-aquae Illiger, 1802
Semblis marginata Panzer, 1804
Ephemera swammerdiana Latreille, 1805
Ephemera swammerdamiana Shaw, 1806
Palingenia longicauda (Burmeister, 1839)

Material and methods

I started my study on the life history and distribution of larvae of *Palingenia longicauda* along the Bulgarian Danubian stretch in September, 1952. For my qualitative and quantitative surveys I used the so-called fisherman's probe or gunter, utilized by sportsmen for collecting mayfly larvae as bait. This is a metal cylinder, measuring 16—18 by 32—34 cm, fixed on a wooden handle of 6—8 m long. In total 1033 larvae and nymphs were collected from 22 localities along the Bulgarian bank of the Danube (table 1).

The transversal distribution of larvae of *Palingenia longicauda* was established during several years of zoobenthal studies along and across the river between km 845 and 375. These studies were carried out aboard of the hydrographical ship "Ossum", property of the Bulgarian Danube Shipping and Monitoring Au-

Table 1. Larvae and nymphs of *Palingenia longicauda* on the clay bottom immediately by the right Danubian bank.

Date	Locality (river km)	Total No of individuals	Average body length (cm)	Average length of caudal filaments (cm)	Average body width (cm)	Average body weight (mg)	Average number (ind/m²)	Average biomass (g/m²)
1.10.52	498	20	3.7	0.8	0.7	254	1100	279
12.09.53	497	4	4.4	1.1	0.7	331	Qualitative sample	
6.07.54	475	15	4.0	1.1	0.6	297	248	74
23.09.54	436	204	3.4	0.8	0.5	174	1625	286
28.09.54	789	17	4.3	0.9	0.6	403	846	341
29.09.54	745	9	4.5	1.1	0.7	388	Qualitative sample	
30.09.54	715	31	4.2	0.6	0.6	350	1755	615
1.10.54	678	6	4.0	1.1	0.6	301	298	90
16.10.54	555	19	3.8	0.5	0.6	242	473	115
22.10.54	475	100	3.8	0.7	0.6	192	1244	239
24.10.54	527	27	4.0	0.6	0.7	282	697	190
18.03.55	475	106	4.3	0.9	0.6	250	1294	330
18.03.55	436	12	4.2	1.1	0.6	279	176	49
14.06.55	475	57	3.0	1.3	0.6	330	1045	345
19.06.55	516	38	3.3	0.7	0.5	179	1631	293
13.09.55	544	14	3.4	0.8	0.5	224	550	123
14.09.55	666	16	3.5	0.8	0.5	216	Qualitative sample	
20.09.55	383	56	4.4	1.1	0.6	384	1485	593
20.09.55	376	3	4.3	1.1	0.6	343	Qualitative sample	
21.09.55	436	38	3.8	1.1	0.6	296	614	183
9.01.58	517	234	3.3	1.1	0.6	414	1045	433
17.10.59	715	7	3.3	1.1				
		1033				Average:	949	269

thority, Russe. The precise data (within 1—2 m) of the position of the ship at each site were obtained by trigonometric methods; also data on the amount of water as well as the current velocity at the surface and every second meter down to the bottom were provided by the authorities. Zoobenthos was collected by means of a Petersen's bottom sampler (1/10 m²).

From 1956 to 1973 the Bulgarian stretch of the Danube was surveyed at 1036 sites; *Palingenia* was collected at 37 of these (table 2). Sixty-five observations were carried out on the metamorphosis of the nymph, the moulting of the subimago and the flight of the adults at various localities of the Bulgarian Danube (table 3). The stomach content of 387 sterlets (*Acipenser ruthenus* (L.)) obtained from fish markets all the way from Vidin to Silistra, as well as during the actual fishing with fishing rods and nets, was studied between 1953 and 1958 in order to find out the significance of the zoobenthos and particularly of *Palingenia longicauda* for the nutrition of this and other fish species. The laboratory and statistical analyses were done according to Russev (1963).

Ecology and life history of aquatic stages

Our studies showed that a fertilized female of *Palingenia longicauda* produced 8—9000 eggs (Unger, 1927, estimated some 7000 eggs per female). The eggs were carried downstream for kilometres due to the high current velocity of the river (over 1 m/s), the average water depth of 7—8 m, and the fact that they are sinking slowly.

Quantitative studies along and across the river (Russev, 1978) revealed to a certain extend the fate of the young larvae after they had reached favourable or less favourable substrates (table 2). No larvae were ever found in sandy substrate, only two on sand-and-clay, and one on both gravel-and-sand and mud-and-sand. They were more frequent in gravel and gravel-with-corophium-mud or cinder (13 times, 7.0% of the samples in this biotope), and in clay (19 times, 40.6% of the samples in this biotope). The frequency of occurrence in the entire stretch studied amounted 3.6% (Russev, 1967), thus indicating the significance of the clay substrate for larval development. As the clay is located near the

banks the distance from the banks can be considered a key, although indirect, ecological factor, affecting the distribution (Russev, 1977).

The larvae were predominantly found up to 100 m from the Bulgarian bank (70% of the localities), seven localities (23%) were between 100 and 252 m and two (7%) between 789 and 880 m off the Bulgarian bank. This shows the inability of the larvae to maintain their positions at distances of more than 250 m from the banks, which should be attributed to the higher current velocity and the inadequate sand substrate in the middle of the stream. No larvae were found at flow rates over 0.76 m/s (measured 0.5 m above the bottom) and on sandy substrate.

Depth is hardly of influence on larval distribution. Larvae were found at depths of up to 10.6 m. During periods of rapid fall of the water level (e.g. on 29 September, 1954) they left their holes in the clay, while many of them died while they tried to follow the retreating water.

The studies on the horizontal and vertical distribution of larvae of *Palingenia longicauda* at km 166.5 of the Tissa river led to the conclusion (Csoknya & Halasy, 1974), that "... the most uniform distribution of the zoobenthos is found 5 m from the bank towards the river bed, in the entire depth of the mud samples (60 cm). In the region lying closer to the bank (3 m) the young larvae (0.5—20.5 mm) are distributed fairly uniformly in the mud samples. Between 3 and 7 m from the bank, however, they occurred in the uppermost 20 cm layer. The largest larvae (40.5—60.5 mm) are more frequent 4—5 m from the bank, and predominantly in the mud layers (30—50 cm). Intermediate larvae (20.5—40.5 mm) exhibit a uniform distribution in the region examined".

During our studies on *Palingenia longicauda* we measured the following hydrological and hydrochemical parameters: average current velocity ranging from 0.56 to 2.10 m/s; turbidity 13—1046 g/m^3; floating deposits 37—8391 kg/s; transparency 0.9—23 cm; temperature up to 28.2 °C; dissolved oxygen 5.55—9.65 ml/l; oxygen saturation 68—123%; oxydability 2.41—9.40 mg/l 0_2; biological oxygen demand for five days (BOD_5) 5.74—0.35 ml O_2/l; total hardness 7.67—13.7 dH^0; pH 7.5—8.2; alkalinity 2.00—3.06 mg equiv./1; HCO_3 124.0—186.9 mg/l; Cl' 11.8—17.5 mg/l; general mineralization 239—439 mg/l (Russev, 1968).

According to Swammerdam (1752), Unger (1927) and Schoenemund (1929) the larvae of *Palingenia longicauda* feed on the organic matter, which is taken up by the stomach from the clay that is consumed. Strenger (1973) noticed that the mouth organs of *Palingenia* are well adapted for scratching the detritus.

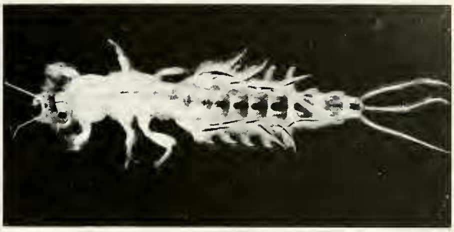


Fig. 1. Larva of *Palingenia longicauda* (Photo A. Valkanov).

Only eggs that have reached adequate clay substrate, develop normally. Under laboratory conditions at water temperatures of 20—25 °C Unger (1927) found out that the embryonal development up to the hatching of the larvae lasted for 4—6 weeks. He assumed that larval development took three years, and because of continuous growth, the larvae passed through some twenty moultings. Already Swammerdam (1752) made the observation of three different size classes of larvae shortly before the metamorphosis, from which he concluded that their longevity was three years. We tried to distinguish the respective stages by biometrics and analysis of variance between larvae of various ages, but we obtained no positive results. This was obviously due to individual and nutritional peculiarities of larvae of various ages leading to merging sizes and weights within the various age groups. Only in July, shortly after the emergence of the adults but before the hatching of the young larvae, two age groups could be distinguished, which confirmed the three-year life-cycle. In other cases we have observed just one age group after emergence. The probability of absence of a certain age group at a particular site is very high, since new eggs do not reach all localities each year.

The larvae live in U-shaped holes dug in the clay. They make these holes using their well-adapted legs. Particularly the forelegs provided with denticles on the lateral sides, as well as the mandibulae with their strong lateral chitine denticles, are very suitable for digging (fig. 1). According to Swammerdam (1752) these holes are "... lange, und rechte, zuweilen aber auch krumme und schiefe hohle Röhren in Thone,

Table 2. Distribution of *Palingenia longicauda* larvae across the Danube off the Bulgarian river bank (samples collected from a ship by the Petersen Bottom Sampler. 1/10 m^2).

Date	km	Distance off the bank	Depth (m)	Substrate	Water temp.	Vbot. (m/s)	ind./ m^2	Weight/ m^2	Average weight (mg/ind)	Average length (mm)
3.04.61	516	15	4.80	clay	11.2	0.76	46	1141	25	9.9
4.04.61	552	880	7.20	clay	11.2	0.76	110	4565	41	13.7
19.04.61	381	52	2.90	clay	16.8	0.73	27	1214	45	16.3
13.04.64	704	15	5.20	clay and mud	11.0	0.60	27	5400	200	24.5
14.04.64	693	252	3.40	clay and mud	11.4	0.60	5	1800	360	29.2
					Average:		43	2824	134	18.7
6.04.61	661	15	6.40	gravel, coroph. mud	11.6		18	475	26	12.3
17.04.64	563	75	3.70	gravel, clay	12.2	0.74	3	458	153	
15.04.58	747	300	9.80	gravel	9.0			body parts		
15.04.58	747	150	7.00	gravel	8.9			body parts		
					Average:		11	467	90	12.3
2.06.59	381	52	8.00	clay	20.2	0.76	18	667	37	16
14.06.60	381	45	4.20	clay	22.0		9	27	3	
10.07.68	599	2		clay	26.7		2	27	14	9
3.06.59	432	50	6.00	clay and sand	21.7		9	849	94	19
13.07.64	588	15	1.00	clay	23.7			Qualitative sample		
					Average:		10	228	19	12.5
14.07.64	552	123	5.00	gravel, sand	23.8	0.51	9	164	18	9.2
26.06.60	665	40	10.60	coroph. mud gravel	21.8		9	849	94	19
27.09.56	381	25	6.50	clay	16.7		27	1408	52	15.3
19.10.58	536	15	5.20	clay	13.2		27	183	7	9
19.10.58	523	15	4.70	clay	12.9		27	183	7	10
2.09.60	381	783	2.90	clay	23.2	0.57	119	1488	13	11
2.09.60	381	41	2.80	clay	23.2	0.64	18	180	10	11
15.10.64	693	458	3.10	clay	15.4	0.88	37	2356	64	17.3
23.10.64	381	57	3.30	clay	15.0		237	3588	15	10.91
7.10.56	678	100	5.00	clay and sand	17.0		5	676	135	27
14.09.57	747	15	3.20	clay and gravel	20.9		3	137	46	18
					Average:		56	1133	39	14.5
27.09.56	381	38	8.32	gravel	16.5		9	430	48	26
14.09.57	747	73	2.72	gravel	20.8	0.54	9	55	6	17
10.10.58	747	101	2.90	gravel	17.2	0.43	3	92	31	12.8
22.10.58	432	40	2.50	gravel	12.6		18	174	10	10
9.10.59	678	15	5.60	gravel and cinder	16.5		5	265	53	
15.10.58	678	15	5.60	gravel and cinder	15.9		9	128	14	8.5
					Average:		9	191	27	14.9

(Table 2, continued)

Date	km	Distance off the bank	Depth (m)	Substrate	Water temp.	Vbot. (m/s)	ind./ m^2	Weight/ m^2	Average weight (mg/ind)	Average length (mm)
9.10.56	747	73	2.72	coroph. mud, gravel	15.3		18	59	3	
10.10.58	747	15	3.20	coroph. mud, gravel	17.2		18	694	39	18
12.10.58	834	107	2.50	coroph. mud, gravel	17.3	0.43	5	206	41	17
19.10.64	552	121	3.50	coroph. mud, gravel	15.4	0.34	9	182	20	8.7
18.09.65	747	105	4.90	coroph. mud, gravel	19.0	0.62	Qualitative sample			
13.10.64	747	689	2.70	mud. fine sand	15.4	0.30	9	274	30	10
					Average:		12	283	27	13.4

die sich nach Grösse und aus dem Anwachsen ihrer Leiber immer weiter und grösser machen".

Using a fisherman's probe on July 14, 1956, between two islands at km 475 of the Danube river, we dug out a well-preserved U-hole, which was 25 cm long, 10 mm in diameter at the arch and 8 mm at the straight sections. It may have housed a metamorphosing nymph that had emerged the previous day, when we observed a mass flight of *Palingenia*. Usually the larval holes were 10—15 cm long and 6—8 mm wide. The larvae maintain a constant water and oxygen inflow, as well as excrement and CO_2 outflow by regular wave-like movements of the body and the tracheal gills. The larvae stay in their holes during daytime, while at night they move around searching for food or a better site (Bačescu, 1943). We were unable to capture one single larva during our multiple attempts with Bačescu's catching device.

During very low water level in fall, we have observed small areas of the clay bottom densely covered with holes of *Palingenia*, e.g. 2000—4500 holes/m^2 (12 September, 1952 at km 497), 1200 holes/m^2 (28 September, 1954 at km 789) and 6700 holes/m^2 (14 September, 1955 at km 666) (fig. 2). This means densities of up to 3350 larvae per m^2.

Our studies revealed that the right bank of the following stretches were particularly rich biotopes for *Palingenia*: km 380—383, km 435—437, km 470—478, km 515—540, km 556—558, km 714—716 and km 830—836. The average larval density amounted to 949 specimens/m^2, and the average biomass to 269 gram/m^2 (table 1). The average larval density in the Kilian branch of the Danube, as observed by Markovskii (1955), was 360 specimens/m^2, and the average biomass 5.16 g/m^2. He also recorded a presence in the biocenosis of 100%, and a density index of 22.7. Csoknya & Ferencz (1972) found an average larval density at the first and 2nd km of the Maroš river of 89.7 specimens/m^2, and of 17.5 specimens/m^2 between km 170—171.5 in the Tissa river.

Larvae of *Palingenia longicauda* were the dominant and most typical representative of the argylorheophilous biocenosis in the Danube river off the Bulgarian bank.

ECOLOGY AND LIFE HISTORY OF FLYING STAGES

We have observed the flight of *Palingenia longicauda* between June, 1955 and June, 1968 along nearly the full Bulgarian stretch of the Danube (km 845—375), as well as at the river mouths of the Iskar (Danube km 640) and the Yantra (Danube km 537) (table 3).

Ethology and metamorphosis of nymphs and subimago. — The nymphs, after leaving their

Table 3. Observation on the flight of *Palingenia longicauda* over the Danube between the 845th and 375th km.

Date	Locality (river km)	Time of beginning	Time of mass flight	End of flight	Abundance estimates	Air temp.	Water temp.	Direction and strength of wind	Clouds	Source
20.06.49	556				mass					Vl. Beshkov
15.06.55	475	16	17	18.15	medium	21.5°	20°	0.00	2/0	ours
15.06.55	527				mass					fishermen
17.06.55	517	14.30	—	16	single	25.5°	21.7°	SSW^{1-2}	5/0	ours
07.06.56	536		—		single		20.0°			fishermen
10.06.56	434		—		single		21.2°			fishermen
11.06.56	381		—		single		21.4°			fishermen
12.06.56	381		—		single		22.2°			fishermen
14.06.56	475-495	13.30	—	19.30	medium		22.8°		80	fishermen
15.06.56	517	15.30	17.15	19.30	abundant	25.5°	24.5°		55	fishermen
16.06.56	517	17	17.30	19.45	medium	21°	23.9°		74	fishermen
13.06.57	834	15			single		21.1°			N. Mladenov
14.06.57	747	15	16	19	mass		21.2°			N. Mladenov
15.06.57	747	15	16	19	mass		21.6°			N. Mladenov
05.06.58	396-385	17	—		single	23°	21°			ours
	377-376		—		single					ours
06.06.58	396	15	—		single	16.3°	22.4°			ours
06.06.58	415	17.30	—	19.30	single	19°	23°	NW^{2-3}	10/4	ours
08.06.58	597-554	17.30	—	18.30	medium	17.2°	21.1°			N. Mladenov
08.06.58	527-544				mass	19.4°	21.4°	0.00	0/0	crews
09.06.58	523-548	16.25	17.30	19.30	peak	23.5°	21.4°	0.00	0/0	ours
10.06.58	536-544				mass	20.3°	21.4°	0.00	0/0	fishermen
11.06.58	519-536	16.20	18.30	20	medium	25.1°	22.3°	E^{3}	8/0	ours
12.06.58	536	16.20	18.30	20	mass	25°	23°	0.00	3/0	ours
04.06.59	536	15.30			single	14.4°	19.6°	NE^{3}		ours
05.06.59	536	15.30	17	18.30	mass	13.4°	18.7°			ours
06.06.59	536	15.30	—	18.30	single	16.2°	18.6°		10/10	ours
07.06.59	544	17	—		single	18.6°	19°			ours
08.06.59	536	17	—	19	single	19.6°	19.8°	E^{3-4}		ours
09.06.59	536	17	—	18.30	single	19.6°	21.2°	E^{1-2}	6/4	ours
11.06.59	600		—		single	18.4°	20.4°			ours
31.05.60	536				single	18.1°	18.4°			fishermen
04.06.60	536	16.20	—	19	single	25°	20.5°	W^{2}	3/2 58	ours
05.06.60	536	16.10	—	17.30	single	22°	21.5°	0.00	8/0	ours
07.06.60	715	16	—	—	single	18.6°	20.5°	E^{3}		ours
09.06.60	715	16.30	17	19	mass	19.6°	21.1°			ours
10.06.60	715	16.30	17	19	mass	20.3°	22°			ours
11.06.60	715	—	—	—	—	16.4°	18.8°	W^{4}	10/10	ours
24.06.60	616-620	18	—	19	single	17.5°	20°			ours
27.06.60	714	18.30			single	25°	22.4°	0.00	7/0	ours
01.06.61	585									N. Mladenov
05.06.61	455	17	—	18	single					N. Mladenov
05.06.61	516-544	15.30		18	single				75	ours
06.06.61	423-434				single					N. Mladenov

(Table 3, continued)

Date	Locality (river km)	Time of begin-ning	Time of mass flight	End of flight	Abun-dance esti-mates	Air temp.	Water temp.	Direc-tion and strength of wind	Clouds	Source
07.06.61	454	16.30	17.30	18	medium					N. Mlade-nov
07.06.61	520-536	16	18	19	medium	23.5°	20.5°	E^3	68	ours
08.06.61	536	16.30	17.30	19	medium	21-	20.5°		98	ours
09.06.61	527-541	16.45		18.15	single	22.5°	20.5°	SW^2	82	ours
17.06.61	834	17.30			single					N. Mlade-nov
20.06.61	600				single					N. Mlade-nov
07.06.63	743	17.30	—	19	single		20.8°			ours
08.06.63	747	12	17	19.30	medium		21°			ours
09.06.63	568-554	16	17	19	abundant					ours
15.06.65	565-589	17.20	18.20		mass			wind	clouds	W. Naide-nov
16.06.65	678	17			single					N. Mlade-nov
16.06.65	555	17	18.30	19.30	medium					W. Naide-nov
18-20.06. 65	834				single					N. Mlade-nov
01.06.66	742-744	16	—	18	single					N. Mlade-nov
01.06.66	670		16		mass					fishermen
2-5.06.66	743-495				single	cold		wind	10/10	N. Mlade-nov
06.06.66	478-473	16.25	17.30		few					N. Mlade-nov
07.06.66	434	17.30			single					N. Mlade-nov
10.06.66	470	18.30			single					N. Mlade-nov
28.05.68	576				medium					N. Mlade-nov
29.05.68	570				mass					N. Mlade-nov

U-shaped holes, emerge at the water surface. Within a few seconds the head and thoracal skin cracks and the winged insect flies out (fig. 3). The larval exuviae are carried away by the stream. The females always complete metamorphosis at the water surface, while male subimagos were usually observed flying directly out of the water. The metamorphosis of the male nymph presumably takes place while it is moving to the water surface. The flying male subimagos reach the river bank, where they attach to trees, grass, bottom, buildings etc. Within seconds they moult again, and the imago leaves the subimaginal skin. This is a critical moment in its life, since the entire muscle system participates in the moulting, which is accompanied by a tremour of the body. At the beginning the insect is somewhat stiff. The moulting then goes through the following fases, (a) the wings are brought together at an angle of less than 40°, (b) the legs are bent under the thorax, while the latter is raised above the level of the abdomen, (c) the head is bent downwards, (d) meanwhile, beginning from the final abdominal segment and the caudal filaments, the moulting takes place and the wings and thorax are gradually released. Wing moulting is much slower than that of the thorax, and the white skin can be observed while

Fig. 2. Holes of *Palingenia longicauda* larvae in a clay bank of the Danube river at km 715 (Photo B. Russev).

it is removed from the base to the apex of the wing. During the moulting of the legs, the insect loses its equilibrium and falls sidewards. After releasing wings and legs, the imago makes intensive movements for the complete release of the caudal filaments and the entire body from the exuviae (figs. 4—10). Unsuccessful moultings were seen very frequently.

Ethology of imagos. — The newly emerged male imago is more active and flies much faster than the subimago. Its caudal filaments are about three times as long (ca. 65 mm), the forelegs are longer and its yellowish-brown coloration is much brighter. Males usually fly towards the middle of the stream searching for females, whereafter they either return to the bank or fly further upstream. In the latter case they make the 45° turn until they take the downstream direction again. The movements and body position of males searching for females is most typical. The two caudal filaments are stretched sidewards at an angle of 45° towards the body, thus forming an angle of 90° between themselves. The forelegs are stretched forewards resembling horns. The caudal filaments often touch the water surface, when the male flies low over the water surface. When a female emerges, a cluster of up to ten competing males may approach it. Males seem to emerge one hour before the females, while they also frequent the banks. This may lead to the wrong conclusion that males are more numerous than females. As was already observed by Swammerdam (1752), Cornelius (1848) and Csongor & Moczar (1954) females do not have a subimago stage. This may be the reason why they moult somewhat later. The females may be easily distinguished by their larger body, large white wings, smaller eyes, and three times shorter caudal filaments. They fly higher and faster than males. Although we have observed matings in flight, gradually losing height, most matings

were seen on the water surface. Drenkelfort (1910, cited after Brinck, 1957), however, considered mating at the surface exceptional. During copulation the position of the male is under the female, while he holds her head with the forelegs. Couples may fly in any direction. According to Brodskii (1973), in his work on the swarming behaviour of mayflies, species of the family Palingeniidae show the very abundant third swarming type; the male's mating flight includes rapid horizontal flight parallel to the water surface.

Mass flights. — During mass flights the abundance of males and females gradually increases, and may reach more than 120 individuals/m^3. The river turns brown and even darker strips and spots may be detected. A typical buzz of hundreds of thousands of wings can be heard and a fish odour be smelled. Most specimens fly between one and three m above the surface. After the mating the males fall at the water and are carried away by the stream. The fertilized females continue their short life until they have layed their eyes. Mass flights seldom last more than half an hour.

After mass flights the banks are covered with subimaginal skins and look white (figs. 11—13). The water surface is still covered with skins, and exhausted males still moving their wings.

Compensation flights. — After the mating the females fly upstream with c. 18 km/h (Russev, 1959). Males that were unable to mate also do so, but usually at a lower speed of 14 km/h (figs. 14, 15). Females may sometimes touch the water, and fly off again without getting drowned. We have observed, under experimental conditions, that females oviposit immediately after a dropping by wave-like movements. The total number of eggs laid numbers appr. 8—9000, which all get dispersed in the water.

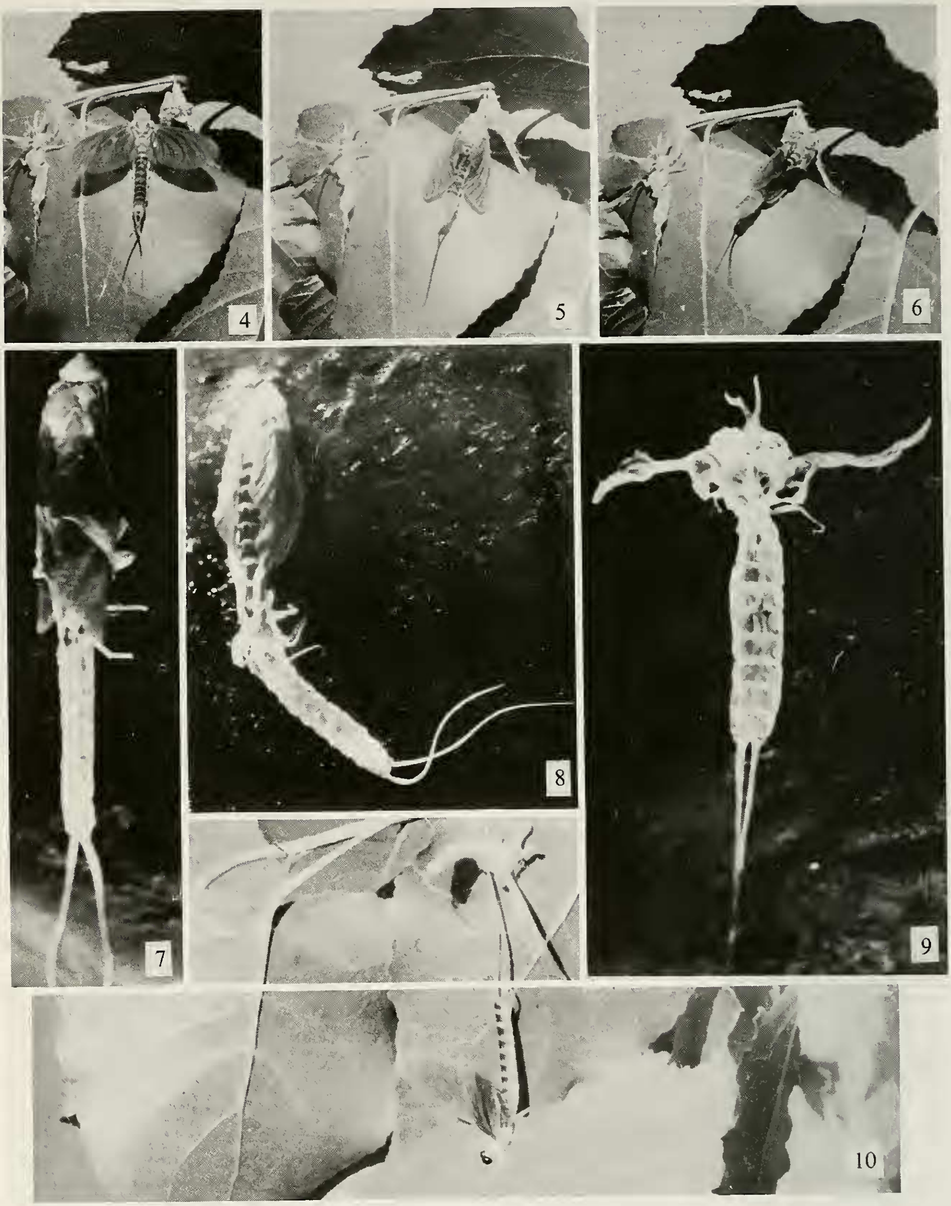
We have called the upstream flight of the fertilized females the "egg-laying-preceding compensation flight" (Russev, 1959). This adaptive behaviour may compensate the downstream movements of the nymphs during metamorphosis, as well as the carriage of the eggs by the water current before they reach the bottom. Eggs are very small (360/300 to 380/330 µm, see figs. 16—20) and may be carried ca. three km (Russev, 1973). This is corresponding to the "colonization cycle" concept of Müller (1954), and confirmed by other studies (Müller, 1973, 1982; Keller, 1975, and others).

Fig. 3. Mass metamorphosis of nymphs of *Palingenia longicauda* on the water surface of the Danube river (Photo B. Russev).

Ecological factors. — The ecological factors that influence emergence and development of the adult stages are not fully clear. The compensation flight is strongly influenced by strong winds. This was clearly observed in June 1960 at km 715. After mass flights on the 9th and 10th, there was not a single mayfly on the 11th with poor weather and strong western wind. The flights resumed after June the 20th under more favourable weather conditions (table 3). Another example dates from June 1958 at km 536. *Palingenia longicauda* was most abundant on the 8th, 9th, 10th and 12th during calm, sunny and warm weather, whereas the flight was of medium intensity on 11th, with a wind of 3 Beaufort.

During a gentle breeze (3 Beaufort or less), fertilized females can still perform their compensation flight, as already described by Russev (1973, figs. 3—5). It seems that wind direction does not influence these flights, as could be concluded from observations where the stream followed a west-east (fig. 5), or northwest-southeast direction (at km 716 and 556), or any other direction. Orientation seems to be guided by the oculi, or, as was noted earlier by Russev (1959), by brief touches of the water surface, where the insects may be able to detect the current direction. Further studies are, however, needed to find out the exact orientation mechanism. The larger weight and wings, as well as the shorter caudal filaments of the females may be considered as morphological adaptations for carrying eggs, as well as for the compensation flight.

Influence of light intensity on swarming, as was proposed by Pongracz (1933, cited after Csongor & Moczàr, 1954), should be investigated further, and the same is true for Csongor & Moc-



Figs. 4—10. Stages of moulting of the subimago of *Palingenia longicauda* (Photos B. Russev).

Figs. 11—13. Subimaginal exuviae of *Palingenia longicauda* on the bank of the Danube river (Photos B. Russev).

Figs. 14—15. Upstream compensation flight of *Palingenia longicauda*. Danube river. (Photo B. Russev).

sàr's statement that "the coincidence of high atmospheric pressure, high water and air temperature, with changing moon phase furthers mass emergence". According to our observations in the period 1955—1958 mass flights in the Danube coincided with the last quarter of the moon (13 June, 20 June and 9 June, respectively), but we do not consider this clear proof.

We also tried whether summarized water temperatures affected the timing of swarming. The average water temperature at the town of Svishtov was calculated for the period 15 June 1955 to 9 June 1960, but no correlation was found between annual averages and the timing of the flights.

Flight period. — Mass flights of *Palingenia longicauda* off the Bulgarian bank in the Danube were observed between 8 and 15 June; the entire flight period lasted from 5 to 20 June. Only very few observations are available outside this period. A medium to mass flight was observed on 28 and 29 May, 1968 at km 576 and km 570 by eng. N. Mladenov (personal communication) (table 3). These observations confirm the period of records of mass flights by Swammerdam (13 June 1671), Triebke (1840) (middle of June), Cornelius (1848) (12—20 June), DzięDzielewicz (1867) (10—25 June), Selys Longchamps (1888) (10—25 June), Moczary (1900) (10—20 June) and Unger (1927) (5 June—early July), but is somewhat different from Beretzk et al. (1957) (end of June—early July, and sometimes even somewhat later). Swammerdam (1752) and Cornelius (1848) considered warm winters, hot springs (particularly May), and limited precipitation favourable for early timing of flights. The abundance of the flights varies from year to year.

Table 4. Literature data on the use of *Palingenia longicauda* as food of various fish.

	Unger (1927) Hungarian Danube	Dimitriu (1937) Romanian Danube	Ferencz (1956) Tissa River	Jancovič (1958) Yougoslavian Danube	Kolarov (1959). Russev (1963) Bulgarian Danube	Gheracopol & Selin (1968) Romanian Danube	Gheracopol et al. (1970) Romanian Danube
Acipenser gueldenstaedti Brand					x		
Acipenser ruthenus (L.)	x	x	x	x	xx	x	
Acipenser stellatus Pall.			x		x		
Ameirus nebulosus Le Sucur			x				
Barbus barbus L.	x		x		x		
Cyprinus carpio L.			x		x		
Esox lucius L.			x		x		
Gymnocephalus cernuus (L.)	x						
Gymnocephalus schraetzer (L.)	x						
Huso huso (L.)					x		
Silurus glanis L.			x				
Stizostedion lucioperca (L.)			x		x		
Zingel streber (Siebold)	x						
Zingel zingel (L.)	x						x

In some years, e.g. 1961, no mass flight was seen at all (table 3).

Flights in Bulgaria were observed between 15.30—19.30 h (sunset on 12 June is at 19.45 h), usually with the following sequence. Metamorphosis of nymphs and male subadults occurred between 15.30—17.00 h; female adults emerged between 16.00—17.00 h; mass flights were between 17.30 and 18.00 h, and compensation flights started after 18.00—18.30 h. Flights started earlier or later only very seldom.

Imago and subimago usually live not longer than two hours, provided that they have mated. Cornelius (1848) noted an adult longevity of 1.5 hours, or up to 13 hours if males had not mated.

Significance of *Palingenia longicauda* for fish nutrition

Palingenia has extensively been used as fishing bait. It has various local names, e.g. "oeveraas" and "haft" in The Netherlands, "Spork-Oese", "Sprock", "Spaargoos","Spaargaänse" in Germany (Westfalen), "Tiszavirag", "Theissblüte" in Hungary, "Vetritze", "Rusalii" in Romania, and "gandatsi" (for the larvae), "rusalki" and "karchani" (for the adults) in Bulgaria. Szent-Ivany & Ujhazy (1973) reported on New Guinean and Hungarian folk songs devoted to mayflies. Two Hungarian folksongs are about the "Flower of the Tissa" (*Palingenia longicauda*).

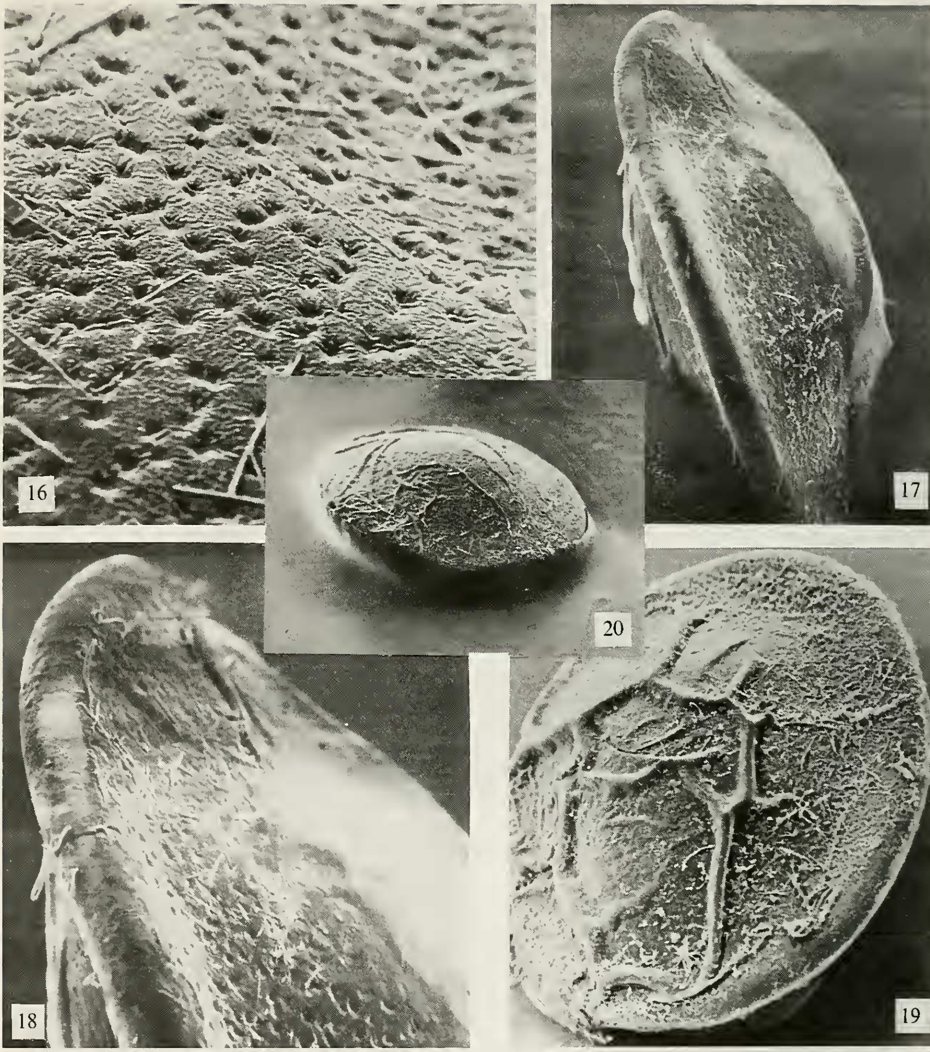
Several authors have reported on the use of larvae of *Palingenia* as baits for fishing sterlet (*Acipenser ruthenus* (L.)), and barbel (*Barbus barbus* L.), *Lota lota* L., *Silurus glanis* L., *Aspro cingel* L., *Chalcalburnus chalcoides danubicus* Antipa and *Cyprinus carpio* L. (Swammerdam, 1752; Antipa, 1909: 248; Băcescu, 1943; Csongor & Moczàr, 1954; Russev, 1956). Bulgarian fishermen were using larvae of *Palingenia* as baits from May to September, and sometimens during winter at low water level, for fishing *Lota lota* and also sterlet. Larvae were collected using the fisherman's probe (gunter). Larvae can be kept alive for several days in cool, moisty sand.

The significance of *Palingenia longicauda* for fish nutrion in the Balkans has extensively been studied (table 4).

Several studies revealed that *Palingenia* dominates in the diet of fishes. In a study of Gheracopol & Selin (1968) and Gheracopol et al. (1969) in the Danube river 69.4% of the diet of the starlet consisted of this mayfly species. An average of 30—40% of the food weight of fishes was found in many other studies (e.g. Russev, 1963). Also see fig. 21.

Factors limiting the distribution

Swammerdam (1752) already described the negative influence of climatological factors on the distribution of *Palingenia*: "Diejenigen



Figs. 16—20. Eggs of *Palingenia longicauda* at various magnifications. — 16, 1450 ×; 17, 285 ×; 18, 730 ×; 19, 285 ×; 20, 140 × (Photos N. Hinton).

Dinge, die das Aas an seiner Veränderung hindern, es tödten, seinen Anwachs aufhalten und verursachen, dass es das eine Jahr in geringerer Anzahl und später als im andern hervorkommt sind folgende: Ein harter langer Winter, viel Schnee und Regen, als welche die Röhrgen, darinnen sie leben, zu und wegspülen, und mit Sand bedecken; dessgleichen auch die grossen Dürre, als die sich nöthiget ihre Häusgen zu verlassen, und andere anzubauen und auszubohren". Nowadays we would add the bank slides, the harmful effects of the deposits on the holes during periods of high water level, the high wind and rain during the time of mass flights, when compensation

flights are impossible and the chance of being carried downstream are increased. Negative effects by fishes were already discussed, but also birds and spiders are heavy predators of this species. Mass flights of *Palingenia* were seen to be attacked by birds as spoonbill (*Platalea leucorodia* L.), sparrowhawk (*Accipiter nisus* L.), kittiwake (*Rissa tridactyla*), as well as wild ducks, swallows, sparrows, larks, wagtails, crows, kites and terns (Gorove, 1819; Csongor & Mocsàr, 1954, personal observations).

On 11 June, 1958, on the pier of Krivina Port, as well as in many other cases, I have observed male subadults being trapped in spider webs, and immediately attacked by the spider.

However, anthropogenetic factors have exerted the strongest negative influence on this species. These factors include the construction of canals, dams, reservoirs, hydrodynamic power plants, commercial irrigation pumps etc. Also increasing pollution was detrimentous to the species. Some indirect evidence of this will be discussed in the following chapter.

Distribution in Europe

In several parts of western Europe *Palingenia* was abundant up to the end of the 19th century. Lestage (1937) and Tshernova (1949) already expressed their concern about the process of its extinction in the rivers of western Europe. They also listed the publications with distributional records. In southern and southeastern Europe it occurred in large numbers as late as the 1960's, but its seems that it is now extinct from most localities in Europe.

The following is a survey of all records available, arranged per country. It should be understood that not all records are fully reliable. Records given by Schäffern (1757) and Cremer (1938) probably all belong to *Ephoron virgo* (Oliv.), what may be concluded from the flight period reported. Also records for France and Belgium are doubtful.

The Netherlands: Clutius (1634), Swammerdam (1675, 1737, 1752), Selys Longchamps (1888), Albarda (1888) and Lauterborn (1918, p. 40) — the rivers of Rhine, Meuse, Waal, Lek, IJssel and some of their tributaries.

Hungary: Marsili (1726, p. 125), Gorove (1819), Mocsáry, S. (1875), Mocsáry, A. (1900), Unger (1927), Pongracz (1933 after Csongor-Mòcsàr, 1954), Csongor and Mòcsàr (1954), Beretzk et al. (1957), Csoknya and Ferencz (1972) — the river of Tissa, Mocsàry, S. (1875) — the following tributaries of the Tissa — Maros, Temes, Fehir-Koros; the Danube; the rivers of Zala and Silo; Dudich et al. (1959, p. 235) — the Danube river.

France: Latreille (1805, p. 98) — the Meuse; Hagen (1888); Lestage (1922) — near Cette.

Czechoslovakia: Mocsàry, S. (1875) — the rivers of Raba, Rebtze, Bodrog and Ronva, Ortvay (1902) — the Danube at Bratislava and the March; Zavřel (1905) — the Morava at Hodonin; Zavřel (1934, cited after Landa, 1969) — the lower course of the March and Šamal (1935) — the Morava at Hodonin; Brtek and Rothschein (1964, p. 30) obtained larvae from Komarno; Rothschein (1959) — the Bodrog and its tributaries Uh, Laboree and Latorica (Eastern Slovakia); Soldan (1978) — the rivers of Bodrog, Strena, Tissa, Trakany.

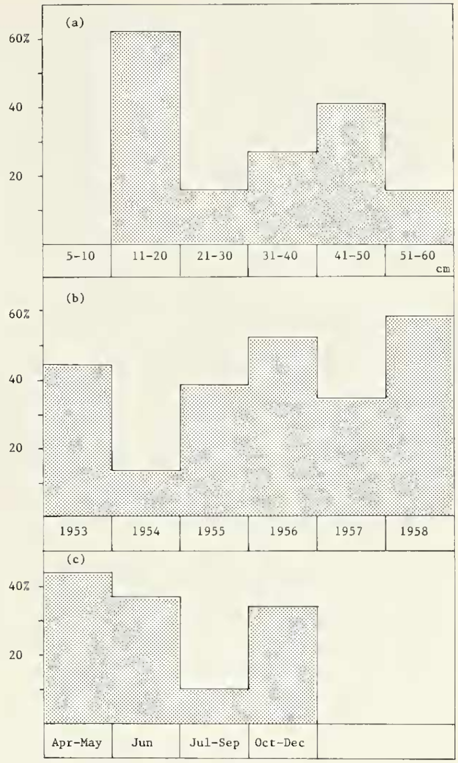


Fig. 21. *Palingenia longicauda* in the diet of sterlet, in terms of percentages of total weight (a) in various size classes of the sterlet, (b) in different years, (c) in different seasons.

Germany: Triepke (1840) — the Oder and some of its tributaries; Cornelius (1848) — the Lippe — a right tributary of the Rhein; Hagen (1859) — Prussia.

The USSR: Dziedzielewicz (1867, p. 161) — the Dnester (upstream from Strvionzh at Sambor town); Kinel, Krasucki, Noskiewicz (1927) — the Dnester; Mikulskii (1936, p. 64) — the Dnester (Strvionzh, Seret and from Lvov downstream); Motaš and Bačescu (1973, p. 29) — 18 km to the east from Kishinev; Tchernova (1949), Markovskii (1955) and Olivari (1961) — the Kilian branch of the Danube.

Romania: Mocsàry, S. (1875) — the Danube at Orsova (The Iron Gates); Motaš (1936) — the Danubian island of Ada-Kale (on the bottom of the present day Iron Gates reservoir); Băcescu (1943) — the Danube, the Prut, the Mureš and the Olt; Bogoescu (1958, p. 58) — the Danube delta, Calaraši and Olteanu at the Danube; Bušnita, Enačeanu and Brezeanu (1961, p. 207) — the Ardjes (a left tributary of the Danube); Bušnita, Brezeanu and Prunescu-Arion (1961, p. 320) — the Olt and the Danube at the Jiul rivermouth; Brezeanu and Prunescu-Arion (1962, p. 167) — the Snt. George branch of the Danube; Enačeanu and Brezeanu (1966, p. 182) — between the 488th and the 235th km of the Danube river; Prunescu-Arion, Elian and Baltac (1965, p. 164) — Măcin branch of the Danube near Braila town; Enačeanu (1967, p. 298 and 416) — the Danube and the flooded lowlands; Bogoescu and Tabacaru (1969) — the Danube delta.

Belgium: Lestage (1923) — "The only known specimen from Belgium was collected some 50 years ago in the vicinity of Diest near Demer".

Poland: Ulmer (1927, p. 240) — the Visla river and some of its tributaries.

Bulgaria: Buresh (1936) — the Iskar river at Svoge; Russev (1956 and 1966) — the Bulgarian stretch of the Danube and channel of the Maritza river.

Yugoslavia: Ikonomov (1958) — the Vardar river, 15 km to the south of Skopje City; Russev (1968) — the Danube.

The data on the distribution of *Palingenia longicauda* in Europe over the last 350 years, reveal that three, not precisely defined, periods can be distinguished. One has to bear in mind, that for many parts of the range insufficient studies are available. The periods are:

1. 1634—1900. *Palingenia longicauda* occurs widely in the lower and middle courses of large and medium-sized rivers,

2. 1901—1927. Its becomes extinct in Western Europe, and is strongly diminishing is Central Europe,

3. 1928—1978. It is still present in the lower course of the Danube river, as well as in the rivers Tissa, Bodrog, Maros-Muresul, Uh, Laboree and Lazorica (all within the water catchment of the Tissa, a left tributary of the Danube), and it was also present in the river Vardar and in a canal near the Maritsa river.

Palingenia used to find favourable conditions in the oligo-β-mesosaprobic water of the Bulgarian Danubian stretch. The gradual deterioration, caused by pollution, led to the rapid extinction of this species. The most abundant flight ever seen was observed in 1958, and before 1968 mass flights were still recorded. Later on the flights became more and more scarce, and over more limited parts of the river. After 1974 no fisherman, crewman of anybody else ever noticed the flight of this popular and large mayfly along the Bulgarian Danubian stretch. Not one single male was seen, nor one single nymph found in clay bottoms of formerly typical localities during a special investigation carried out along the entire Bulgarian bank of the Danube. For this reason, we assume that it has become extinct from this part of the river, as happened in the upper parts of the same river earlier.

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